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# On the reversibility problem of Fleming-Viot processes

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(This talk is based on our joint work with Yao [7].)

## 1 Introduction

Fleming-Viot processes are probability measure-valued diffusions derived as high density limits of discrete particle models in population genetics. The particle models describe the evolution of empirical distributions of the genotypes. The high density limits are more important since they possess richer mathematical structures and there are much more mathematical techniques applicable to them. Because of their importance, Fleming-Viot processes have attracted the research interest of both pure and applied probabilists. A typical Fleming-Viot process is determined by two parameters, the mutation operator and the selection density.

Let  $E$  be a locally compact separable space and let  $M_1(E)$  be the space of Borel probability measures on  $E$  endowed with the topology of weak convergence. We denote by  $B(E)$  the set of all bounded Borel measurable functions on  $E$ , and by  $C_\infty(E)$  the Banach spaces of bounded continuous functions vanishing at infinity if  $E$  is non-compact, which is equipped with the supremum norm  $\|\cdot\|_\infty$ . We denote by  $C_0(E)$  the set of continuous functions with compact support, and by  $C_0^+(E)$  the set of nonnegative functions in  $C_0(E)$ . For  $\mu \in M_1(E)$ , we denote by  $\mu^{\otimes n} \in M_1(E^n)$  the  $n$ -fold product of  $\mu$ . We also use the notation  $\mu(f) := \int_E f d\mu$  for  $f \in B(E)$  and  $\mu \in M_1(E)$ .

Let  $A$  be the generator of a conservative Feller semigroup  $(T_t)_{t \geq 0}$  on  $C_\infty(E)$  with domain  $\mathcal{D}(A)$ , and let  $\sigma = \sigma(x, y)$  be a symmetric bounded Borel measurable function on  $E^2$ . We

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may consider the operator  $\mathcal{L}$  defined by

$$\begin{aligned}\mathcal{L}\phi(\mu) = & \frac{1}{2} \int_E \int_E \frac{\delta^2 \phi(\mu)}{\delta \mu(x) \delta \mu(y)} [\mu(dx) \delta_x(dy) - \mu(dx) \mu(dy)] \\ & + \int_E A\left(\frac{\delta \phi(\mu)}{\delta \mu}\right)(x) \mu(dx) \\ & + \int_E \int_E \frac{\delta \phi(\mu)}{\delta \mu(x)} [\sigma(x, y) - \mu^{\otimes 2}(\sigma)] \mu(dx) \mu(dy),\end{aligned}$$

where  $\delta \phi(\mu)/\delta \mu(x) = \lim_{r \rightarrow 0+} r^{-1} \{\phi(\mu + r \delta_x) - \phi(\mu)\}$ , and the domain  $\mathcal{D}(\mathcal{L})$  is taken to be the set of all  $\phi \in C(M_1(E))$  of the form

$$\phi(\mu) = F(\mu(f_1), \dots, \mu(f_k)),$$

where  $k \geq 1$ ,  $F \in C^2(\mathbf{R}^k)$  and  $f_1, \dots, f_k \in \mathcal{D}(A)$ . A diffusion process  $\{X_t : t \geq 0\}$  with state space  $M_1(E)$  and generator  $\mathcal{L}$  is called a *Fleming-Viot process* with mutation generator  $A$  and selection density  $\sigma$ .

The Fleming-Viot process becomes much more tractable if it processes a reversible stationary distribution. It is well-known that the Fleming-Viot process is reversible if its mutation operator is of the uniform-jumping type:

$$Af(x) = \frac{\theta}{2} \int_E (f(y) - f(x)) \nu(dy), \quad (1.1)$$

which means that the distribution of mutants is independent of the genotype their parents. However, it has been an open problem whether the Fleming-Viot process can be reversible for more general mutation operator; see e.g. Ethier-Kurtz [3].) This problem is solved in the paper [7]. Our result is that if a Fleming-Viot process has a reversible stationary distribution and if its mutation operator  $A$  is irreducible, then  $A$  must be of the uniform-jumping type.

**Theorem 1.1** *Suppose that  $(A, \mathcal{D}(A))$  is irreducible, that is, for every  $x \in E$  and every non-degenerate  $f \in C_0^+(E)$  we have  $T_t f(x) > 0$  for some  $t > 0$ . If the Fleming-Viot process with mutation operator  $A$  and the selection density  $\sigma$  has a reversible stationary distribution  $\mathcal{Q}$ , then  $A$  is of the form (1.1) with*

$$\nu(f) = \int_{M_1(E)} \mu(f) \mathcal{Q}(d\mu). \quad (1.2)$$

In this talk, we shall give the proof of the above theorem in the non-selective case  $\sigma = 0$ . Let us describe a martingale problem formulation for the Fleming-Viot process in this particular case. We denote by  $\Omega$  be the space of continuous paths from  $[0, \infty)$  to  $M_1(E)$  with coordinate process  $\{X_t : t \geq 0\}$  and furnish  $\Omega$  with the compact uniform topology.

Let  $(\mathcal{F}, \mathcal{F}_t)_{t \geq 0}$  be the natural  $\sigma$ -algebras on  $\Omega$  generated by  $\{X_t : t \geq 0\}$ . Then for every  $\mu \in M_1(E)$  there is a unique probability measure  $\mathbf{Q}_\mu$  on  $(\Omega, \mathcal{F})$  such that, for  $\phi \in \mathcal{D}(\mathcal{L})$ ,

$$M_t(f) = X_t(f) - X_0(f) - \int_0^t X_s(Af)ds, \quad t \geq 0, \quad (1.3)$$

is a continuous martingale with quadratic variation process

$$\langle M(f) \rangle_t = \int_0^t (X_s(f^2) - X_s(f)^2)ds, \quad t \geq 0. \quad (1.4)$$

The system  $(\Omega, (\mathcal{F}_t)_{t \geq 0}, \mathbf{Q}_\mu, X_t)$  is a realization for the Fleming-Viot process with mutation operator  $A$ . Moreover, for every  $f \in C_\infty(E)$  we have

$$X_t(f) = X_0(T_t f) + \int_0^t \int_E T_{t-s}f(x)M(dsdx), \quad t \geq 0, \quad (1.5)$$

where  $M(dsdx)$  is the martingale measure determined by  $\{M_t(f) : f \in \mathcal{D}(A)\}$ ; see e.g. [10].

## 2 The non-selective case

Let  $\mathcal{Q}$  be a stationary distribution of the Fleming-Viot process  $(X_t, \mathbf{Q}_\mu)$ . For  $\mathcal{Q}$  we define the moment measures  $m_n$  on the product space  $E^n$  by

$$m_n = \int_{M_1(E)} \mu^{\otimes n} \mathcal{Q}(d\mu), \quad n = 1, 2, \dots, \quad (2.1)$$

and simply write  $m = m_1$ .

From (1.5) it is easy to see that  $m$  is a stationary distribution of  $(T_t)_{t \geq 0}$ . Recall that  $m \in M_1(E)$  is  $(T_t)_{t \geq 0}$ -reversible if and only if

$$m(fT_t g) = m(gT_t f), \quad f, g \in C_\infty(E). \quad (2.2)$$

**Lemma 2.1** *The probability measure  $m$  is  $(T_t)_{t \geq 0}$ -reversible if and only if*

$$m_2(f \otimes T_t g) = m_2(g \otimes T_t f), \quad t \geq 0, f, g \in C_\infty(E), \quad (2.3)$$

where  $f \otimes g(x, y) = f(x)g(y)$ . In particular, if  $\mathcal{Q}$  is a reversible stationary distribution of  $(X_t, \mathbf{Q}_\mu)$ , then (2.3) holds and  $m$  is  $(T_t)_{t \geq 0}$ -reversible.

*Proof.* Applying (1.5) to  $f \in C_\infty(E)$  and  $T_r g \in C_\infty(E)$ , we have

$$X_t(f) = X_0(T_t f) + \int_0^t \int_E T_{t-s}f(x)M(ds, dx), \quad (2.4)$$

and

$$X_t(T_r g) = X_0(T_{t+r} f) + \int_0^t \int_E T_{t+r-s} g(x) M(ds, dx). \quad (2.5)$$

Using the independence of  $X_0$  and  $M(ds, dx)$  and (1.4) to compute  $m_2(f \otimes T_r g) = E(X_t(f) X_t(T_r g))$  we have

$$\begin{aligned} & m_2(f \otimes T_r g) - m_2(T_t f \otimes T_{t+r} g) \\ &= \int_0^t m(T_s f T_{s+r} g) ds - \int_0^t m_2(T_s f \otimes T_{s+r} g) ds. \end{aligned} \quad (2.6)$$

Suppose that (2.3) holds. Interchanging  $f$  and  $g$  in (2.6) we see that

$$\int_0^t m(T_s f T_{s+r} g) ds = \int_0^t m(T_{s+r} f T_s g) ds, \quad (2.7)$$

which yields (2.2). Thus  $m$  is  $(T_t)_{t \geq 0}$ -reversible.

Conversely, if  $m$  is  $(T_t)_{t \geq 0}$ -reversible, then (2.2) holds. Let

$$h(r, t) = m_2(T_t f \otimes T_{t+r} g) - m_2(T_t g \otimes T_{t+r} f). \quad (2.8)$$

By (2.2) and (2.6) it satisfies

$$h(r, 0) = h(r, t) - \int_0^t h(r, s) ds, \quad (2.9)$$

which yields  $h(r, t) = 0$  for all  $r, t \geq 0$ . In particular,  $h(t, 0) = 0$  is the conclusion (2.3).

Finally, if  $\mathcal{Q}$  is a reversible distribution of  $(X_t, \mathbf{Q}_\mu)$ , denoting by  $\mathcal{Q}$  the associated stationary Markovian probability measure on  $\Omega$  with initial distribution  $\mathcal{Q}$ , we have

$$\mathcal{Q}\{X_0(f) X_t(g)\} = \mathcal{Q}\{X_0(g) X_t(f)\}, \quad (2.10)$$

which yields (2.3) because

$$\mathcal{Q}\{X_0(f) X_t(g)\} = \mathcal{Q}\{X_0(f) X_0(T_t g)\} = m_2(f \otimes T_t g). \quad (2.11)$$

Hence  $m$  is  $(T_t)_{t \geq 0}$ -reversible.  $\square$

In the sequel of this section, we assume  $\mathcal{Q}$  is a reversible stationary distribution of  $(X_t, \mathbf{Q}_\mu)$ , so  $m$  is  $(T_t)_{t \geq 0}$ -reversible by Lemma 2.1. Let  $L^2(E; m)$  be the Hilbert space of real-valued  $m$ -square-integrable functions on  $E$  with the inner product  $(f, g)_m := m(fg)$ . Then  $(T_t)_{t \geq 0}$  can be extended as a symmetric contraction semigroup acting on  $L^2(E; m)$ . We denote its generator by  $(\bar{A}, \mathcal{D}(\bar{A}))$ , which is a self-adjoint and non-positive definite operator on  $L^2(E; m)$ . Let  $\mathcal{D}[\mathcal{E}] = \mathcal{D}(\sqrt{-\bar{A}})$ , and for  $f, g \in \mathcal{D}[\mathcal{E}]$  let

$$\begin{aligned} \mathcal{E}(f, g) &= (\sqrt{-\bar{A}} f, \sqrt{-\bar{A}} g)_m, \\ \mathcal{E}_\alpha(f, g) &= \mathcal{E}(f, g) + \alpha(f, g)_m \quad (\alpha > 0). \end{aligned}$$

Then  $(\mathcal{D}[\mathcal{E}], \mathcal{E}_\alpha)$  is a Hilbert space, and  $(\mathcal{D}[\mathcal{E}], \mathcal{E})$  defines an  $L^2$ -Dirichlet space (cf. [6]).

**Lemma 2.2** *As defined above,  $(\mathcal{D}[\mathcal{E}], \mathcal{E})$  is a regular Dirichlet space, that is,  $C_0(E) \cap \mathcal{D}[\mathcal{E}]$  is dense both in  $C_0(E)$  and in  $(\mathcal{D}[\mathcal{E}], \mathcal{E}_\alpha)$ .*

*Proof.* Denote by  $G_\alpha$  the resolvent of  $(A, \mathcal{D}(A))$ . The Feller property of  $(T_t)_{t \geq 0}$  implies  $G_\alpha[C_\infty(E)] \subset C_\infty(E)$ , from which the desired regularity follows. (See [6], Lemma 1.4.2.)  $\square$

For a regular Dirichlet space, it is known that the Dirichlet form has the following expression (cf. [6]).

**Lemma 2.3** *[Beuling-Deny formula] For  $f, g \in \mathcal{D}[\mathcal{E}] \cap C_0(E)$ ,*

$$\begin{aligned} \mathcal{E}(f, g) &= \mathcal{E}_c(f, g) \\ &\quad + \int_{E^2 \setminus \Delta} [f(y) - f(x)][g(y) - g(x)] J(dx, dy), \end{aligned} \quad (2.12)$$

where  $\mathcal{E}_c$  is the diffusion part which satisfies the local property:

$$\mathcal{E}_c(f, g) = 0 \text{ if } f, g \in \mathcal{D}[\mathcal{E}] \cap C_0(E) \text{ and } \text{supp}(f) \cap \text{supp}(g) = \emptyset,$$

and  $J$  is the jumping measure, which is a symmetric Radon measure on the product space  $E^2$  off the diagonal  $\Delta$ .

**Lemma 2.4** *For  $f, g \in C_\infty(E)$ ,*

$$m_2(f \otimes g) = \frac{1}{2} m(f G_{1/2} g). \quad (2.13)$$

*Proof.* Let  $(X_t, \mathcal{Q})$  be the reversible stationary Markov process with initial distribution  $\mathcal{Q}$ . By (1.3) and Itô's formula

$$\begin{aligned} &X_t^{\otimes 2}(f \otimes g) - X_0^{\otimes 2}(f \otimes g) \\ &= \int_0^t \{X_s^{\otimes 2}(Af \otimes g + f \otimes Ag) + X_s(fg) - X_s^{\otimes 2}(f \otimes g)\} ds \\ &\quad + \text{martingale}. \end{aligned} \quad (2.14)$$

Taking the expectation one sees

$$m_2(Af \otimes g) + m_2(f \otimes Ag) + m(fg) - m_2(f \otimes g) = 0.$$

But,  $m_2(Af \otimes g) = m_2(f \otimes Ag)$  by (2.3), so we have

$$2m_2((1/2 - A)f \otimes g) = m(fg).$$

Replacing  $f$  by  $G_{1/2}f$  in the above and using the reversibility of  $m$  we get the desired conclusion.  $\square$

**Lemma 2.5** For  $f \in \mathcal{D}(A)$  and  $g, h \in C_\infty(E)$ ,

$$m_3((I - A)f \otimes g \otimes h) = \frac{1}{2}m_2((fg) \otimes h + (fh) \otimes g). \quad (2.15)$$

*Proof.* We first assume  $f, g, h \in \mathcal{D}(A)$ . Let  $(X_t, \mathbf{Q})$  be as in the proof of Lemma 2.4. By the Markov property and the reversibility of  $(X_t, \mathbf{Q})$  we get

$$\begin{aligned} & \mathbf{Q}\{X_0^{\otimes 2}(f \otimes g)X_0(T_th - h)\} \\ &= \mathbf{Q}\{X_0^{\otimes 2}(f \otimes g)[X_t(h) - X_0(h)]\} \\ &= \mathbf{Q}\{[X_t^{\otimes 2}(f \otimes g) - X_0^{\otimes 2}(f \otimes g)]X_0(h)\}, \end{aligned}$$

from which together with (2.14) it follows that

$$\begin{aligned} & \mathbf{Q}\{X_0^{\otimes 2}(f \otimes g)X_0(T_th - h)\} \\ &= \int_0^t \mathbf{Q}\{[X_s^{\otimes 2}(Af \otimes g + f \otimes Ag - f \otimes g) + X_s(fg)]X_0(h)\}ds. \end{aligned}$$

Then dividing the equality by  $t > 0$  and letting  $t \rightarrow 0$  we get

$$\begin{aligned} m_3(f \otimes g \otimes Ah) &= m_3(Af \otimes g \otimes h + f \otimes Ag \otimes h - f \otimes g \otimes h) \\ &\quad + m_2((fg) \otimes h). \end{aligned}$$

Interchanging  $g$  and  $h$ ,

$$\begin{aligned} m_3(f \otimes Ag \otimes h) &= m_3(Af \otimes g \otimes h + f \otimes g \otimes Ah - f \otimes g \otimes h) \\ &\quad + m_2((fh) \otimes g). \end{aligned}$$

A combination of the last two equations gives the desired result for  $f, g, h \in \mathcal{D}(A)$ . The extension to  $g, h \in C_\infty(E)$  is trivial.  $\square$

**Lemma 2.6** If  $f, g \in \mathcal{D}[\mathcal{E}] \cap C_\infty(E)$  and  $h \in C_\infty(E)$ , then  $fG_{1/2}h, gG_{1/2}h \in \mathcal{D}[\mathcal{E}]$  and

$$\begin{aligned} & \mathcal{E}(g, fG_{1/2}h) + \frac{1}{2}m(fhG_{1/2}g) \\ &= \mathcal{E}(f, gG_{1/2}h) + \frac{1}{2}m(ghG_{1/2}f). \end{aligned} \quad (2.16)$$

*Proof.* The former fact is found as [6, Lemma 1.4.2]. If  $f \in \mathcal{D}(A)$  and  $g, h \in C_0(E)$ , Lemmas 2.4 and 2.5 imply

$$m_3((I - A)f \otimes g \otimes h) = \frac{1}{4}m(fgG_{1/2}h) + \frac{1}{4}m(fhG_{1/2}g).$$

Moreover, if  $g \in \mathcal{D}(A)$ , inserting  $(I - A)g$  in place of  $g$  in the above equation we get

$$\begin{aligned} & m_3((I - A)f \otimes (I - A)g \otimes h) \\ &= \frac{1}{4}m(f(I - A)gG_{1/2}h) + \frac{1}{4}m(fhG_{1/2}(I - A)g) \\ &= \frac{1}{4}m(fgG_{1/2}h) + \frac{1}{4}\mathcal{E}(g, fG_{1/2}h) + \frac{1}{8}m(fhG_{1/2}g) + \frac{1}{4}m(fhg). \end{aligned}$$

Then the desired equality follows from the symmetry between  $f$  and  $g$ . It is trivial to extend for  $f, g \in \mathcal{D}[\mathcal{E}] \cap C_\infty(E)$ .  $\square$

**Lemma 2.7** *The jumping measure  $J(dx, dy)$  of (2.12) is everywhere dense in  $E^2 \setminus \Delta$ , that is,  $J(U \times V) > 0$  for every disjoint non-empty open sets  $U, V \subset E$ .*

*Proof.* Suppose that the conclusion fails. Then there are two non-empty open sets  $U$  and  $V$  such that  $U \cap V = \emptyset$  and  $J(U \times V) = J(V \times U) = 0$ . Now take non-degenerate functions  $f, g \in \mathcal{D}(\mathcal{E}) \cap C_0^+(E)$  and  $h \in C_0^+(E)$ ,  $\text{supp}(f) \subset U$  and  $\text{supp}(g) \subset V$ . Then we have  $\mathcal{E}_c(f, gG_{1/2}h) = \mathcal{E}_c(g, fG_{1/2}h) = 0$  by the local property of  $\mathcal{E}_c$ . It follows that

$$\begin{aligned} & \mathcal{E}(f, gG_{1/2}h) \\ &= \int_E \int_E [f(y) - f(x)][g(y)G_{1/2}h(y) - g(x)G_{1/2}h(x)]J(dx, dy) \\ &= - \int_E \int_E [f(x)g(y)G_{1/2}h(y) + f(y)g(x)G_{1/2}h(x)]J(dx, dy) \\ &= 0. \end{aligned}$$

Similarly,  $\mathcal{E}(g, fG_{1/2}h) = 0$ . Then we get by Lemma 2.6 that

$$m(hfG_{1/2}g) = m(hgG_{1/2}f), \quad h \in \mathcal{D}(A). \quad (2.17)$$

The irreducibility of  $(T_t)_{t \geq 0}$  implies that  $m$  is everywhere dense and  $G_\lambda f(x) > 0$  for all  $x \in E$  if  $f \in C_0^+(E)$  is not constantly zero. Therefore, (2.17) and the Feller property of  $G_\lambda$  imply

$$f(x)G_{1/2}g(x) = g(x)G_{1/2}f(x), \quad x \in E. \quad (2.18)$$

This is a contradiction since  $f$  and  $g$  have disjoint supports while  $G_{1/2}f(x) > 0$  and  $G_{1/2}g(x) > 0$  for all  $x \in E$ .  $\square$

*Proof of Theorem 1.1 in the non-selective case.* We claim that, for  $f, g, h \in C_0(E)$  with mutually disjoint supports,

$$\int_E \int_E f(x)g(y)[G_{1/2}h(y) - G_{1/2}h(x)]J(dx, dy) = 0. \quad (2.19)$$



From the regularity of the Dirichlet form it follows that for every  $f \in C_0^+(E)$  there exists  $\{f_n\} \subset \mathcal{D}[\mathcal{E}] \cap C_0^+(E)$  such that  $\text{supp}(f_n) \subset \text{supp}(f)$  and  $\lim_{n \rightarrow \infty} \|f_n - f\|_\infty = 0$ . Therefore, it suffices to show (2.19) for  $f, g \in \mathcal{D}[\mathcal{E}] \cap C_0(E)$ . Observe that

$$\mathcal{E}_c(g, fG_{1/2}h) = \mathcal{E}_c(f, gG_{1/2}h) = 0 \text{ and } fh(x) \equiv gh(x) \equiv 0. \quad (2.20)$$

Then, by Lemma 2.6,

$$\begin{aligned} & \int_E \int_E [g(x) - g(y)][f(x)G_{1/2}h(y) - f(y)G_{1/2}h(y)]J(dx, dy) \\ &= \int_E \int_E [f(x) - f(y)][g(x)G_{1/2}h(y) - g(y)G_{1/2}h(y)]J(dx, dy), \end{aligned}$$

and hence

$$\begin{aligned} & \int_E \int_E [f(x)g(y)G_{1/2}h(y) + f(y)g(x)G_{1/2}h(x)]J(dx, dy) \\ &= \int_E \int_E [g(x)f(y)G_{1/2}h(y) + g(y)f(x)G_{1/2}h(x)]J(dx, dy), \end{aligned}$$

which yields (2.19) due to the symmetry of  $J$ .

Recall that  $J$  is everywhere dense in  $E^2 \setminus \Delta$  by Lemma 2.7. Then (2.19) and the Feller property of  $G_\lambda$  imply that  $G_{1/2}h(x)$  is constant outside the support of  $h$ . Therefore,  $G_{1/2}(x, K)$  is constant in  $x \notin K$  for every compact subset  $K \subset E$ . It follows that for each compact set  $K \subset E$  there exists a constant  $c(K)$  independent of  $x \in E$  such that

$$G_{1/2}(x, K) = c(K), \quad x \notin K. \quad (2.21)$$

It is easy to see that  $c(K)$  can be extended to a Borel measure on  $E$  such that (2.21) holds for every Borel set. Therefore, there exists a constant  $a \geq 0$  such that

$$G_{1/2}(x, \cdot) = a\delta_x(\cdot) + c(\cdot), \quad x \in E. \quad (2.22)$$

Clearly,  $a + c(E) = G_{1/2}(x, E) = 2$  by the conservativity of  $(T_t)_{t \geq 0}$ , and  $0 < a < 2$  by the irreducibility. From (2.22) and the resolvent equation  $(\lambda - 1/2)G_\lambda G_{1/2} = G_{1/2} - G_\lambda$  we obtain

$$[1 + (\lambda - 1/2)a]G_\lambda(x, \cdot) = a\delta_x(\cdot) + (2\lambda)^{-1}c(\cdot). \quad (2.23)$$

From this and (2.22) it is simple to check that

$$\begin{aligned} Af(x) &= \lim_{\lambda \rightarrow \infty} \lambda[\lambda G_\lambda f(x) - f(x)] \\ &= \frac{1}{2a} \int_E [f(y) - f(x)]c(dy). \end{aligned}$$

Thus  $(A, \mathcal{D}(A))$  is of the uniform jumping type. Since  $m$  is a reversible measure for  $(A, \mathcal{D}(A))$ , it must agree with  $c$  up to a constant multiplication. Therefore the proof of Theorem 1.1 in the non-selective case is completed.  $\square$

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